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Individual-level trait diversity concepts and indices to comprehensively describe community change in multidimensional trait space

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Running title: Individual-level trait diversity indices

Summary

1. Global environmental change can influence ecosystem processes directly or through changes in the trait composition of natural communities. Traits are individual-level features of organisms, and theory predicts that diversity in traits should relate to ecosystem processes. Validated indices that account for both intra- and interspecific

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trait variation in multidimensional trait space are lacking. In this article we highlight how an individual-level perspective requires new concepts for trait diversity (TD) and we validate a set of measures suitable to study trait richness, evenness and divergence at the individual scale.

2. First, we tested a selection of multivariate indices for trait richness, evenness and divergence from the literature (FRic, FEve, FDis and the Rao coefficient) using simulated and real individual-level data. We compared the observed changes in the tested indices with those predicted from their expected/required behaviour (that is, increase or decrease under specific manipulation of community trait structure) and found unsatisfactory results only for FRic and FEve, whereas FDis and the Rao coefficient showed the expected changes.
3. Therefore, we propose two novel concepts and related indices for individual-level trait richness (TOP = Trait Onion Peeling) and evenness (TED = Trait Even Distribution). TOP represents the sum of all successive convex hull areas touching all individuals (points) within a multidimensional trait distribution. TED is a measure of how evenly distributed are individuals within the multidimensional trait space. It is calculated comparing the probability distributions of pairwise distances between individuals and between points of a perfectly even reference distribution. We tested TOP and TED on the same simulated and real data as above, and results indicated appropriate behaviour for TOP (trait richness) and TED (trait evenness).
4. By validating TD indices in an individual-level context, the present study contributes to the expansion of functional ecology towards individual-level dynamics. Future comprehensive investigations of individual trait differences in natural communities

may improve our understanding of the pathways by which environmental changes affect ecosystem functioning through biodiversity change.

Key-words trait diversity, richness, evenness, divergence, individual-level, ecosystem functioning, community ecology, plankton.

Introduction

In the context of global environmental changes, understanding and predicting biodiversity responses and their consequences for ecosystem processes and services is becoming imperative (Hillebrand & Matthiessen 2009; Reiss *et al.* 2009; Cardinale *et al.* 2012). The concept of functional diversity is receiving increased attention, since several studies indicate that it better relates ecological structure with ecosystem functioning compared to taxonomic diversity (Tilman *et al.* 1997; Suding *et al.* 2008; Hillebrand & Matthiessen 2009; Reiss *et al.* 2009; Cardinale *et al.* 2012). Although the term functional diversity is widely used and accepted, we prefer to use the terms phenotypic or trait diversity (TD), unless a direct functional effect can be assessed for the measured traits used to calculate biodiversity indices (Violle *et al.* 2007).

Analytical approaches based on TD are also applied to investigate ecological processes, such as community assembly and species coexistence under different environmental conditions (Pérez-Camacho *et al.* 2012; Bhaskar, Dawson & Balvanera 2014; Price *et al.* 2014), climate change effects on vegetation dynamics (van Bodegom, Douma & Verheijen 2014), resilience of communities (Gerisch 2014), effects of disturbance on ecosystem processes (Grass, Berens & Farwig 2014) and niche differentiation between native and non-native species (Ordonez, Wright & Olff 2010; Whittaker *et al.* 2014).

TD should include both inter- and intraspecific variation in functional traits. Intraspecific TD has been long recognised as important in evolutionary biology, but has only more recently gained attention in ecology (Chesson 2000; Chase & Leibold 2003; Lloyd-Smith *et al.* 2005; Clark 2010; Bolnick *et al.* 2011; de Bello *et al.* 2011; Violle *et al.* 2012; Kremer *et al.* 2014). Intraspecific TD is an important component of overall functional diversity (Carmona *et al.* 2014), plays an essential role in coexistence mechanisms and influences community structure and dynamics (Hulshof & Swenson 2010; Bolnick *et al.* 2011). A particularly topical issue in ecology is the need to relate individual-level variability in functional traits to larger-scale ecosystem processes (Norberg *et al.* 2001; Twining & Baines 2013; Koch, Harms & Müller 2014). Despite the increasing recognition of its importance, intraspecific variation in traits is still largely neglected in ecological studies (Kraft *et al.* 2014). Multiple traits measured community-wide at the individual level are the most promising and straightforward way to combine inter- and intraspecific variation into one single approach (Cianciaruso *et al.* 2009; Fontana, Jokela & Pomati 2014). In this way, individual-level traits may afford an integrated description of community dynamics that combines ecological and evolutionary responses (Loreau 2010). For this purpose it is necessary to translate individual-level trait data into meaningful biodiversity indices.

While the general concept of TD is clear, there has never been agreement on a single TD measure, such that existing measures range from the number of functional groups to metrics involving the calculation of a functional dendrogram or the volume of the convex hull containing all taxa of a community (Petchey & Gaston 2006; Villéger, Mason & Mouillot 2008; Fontana, Jokela & Pomati 2014). Nevertheless, a number of desirable and or necessary properties of TD measures are clear. Generally, TD should be derived from the direct quantification of traits, avoiding the use of surrogate measures, such as the number of functional groups represented in a community (Petchey 2004). Additionally, every single

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organism represents a unique combination of traits (perfectly identical phenotypes are really unlikely to exist in natural populations, even if they belong to the same taxon) and therefore should be taken into consideration when calculating TD (Fontana, Jokela & Pomati 2014). In a context in which continuous trait data (as opposed to nominal/ordinal/binary ones) are rapidly accumulating at the individual-level as a consequence of new measuring technologies, potential indices used to describe individual-level TD have to fulfil some new requirements and criteria: for example individual-level data are larger and more complex than species-level data, determining a series of computational, mathematical and ecological issues (Fontana, Jokela & Pomati 2014).

In our view, summarised in (Fontana, Jokela & Pomati 2014), to take advantage of the information disclosed by measuring traits at the individual level, TD indices should be able to deal with continuous data. TD has to consider simultaneously a multivariate trait-space avoiding the categorisation process that introduces arbitrary and critical decision steps (Petchey & Gaston 2006) and causes loss of valuable individual-level information. Since the number of individuals in a community can be much higher than the number of species, the computational tractability of individual-level TD indices can also be an issue (Fontana, Jokela & Pomati 2014).

Given the conceptual criteria mentioned above, not all the currently published diversity indices may be directly applicable to individual-level trait data (Fontana, Jokela & Pomati 2014). For example, most functional diversity indices proposed in the literature were originally designed for species mean traits, affecting their ability to measure pure TD (Pakeman 2014). Nevertheless, some of these can account for intraspecific trait variation, for example the mathematical decomposition of diversity into intraspecific and interspecific components (Pavoine & Izsák 2014). Another example is represented by Cianciaruso et al. (2009), who proposed to directly use individual-level traits in the calculation of the

previously developed FD index (Petchey & Gaston 2002; Petchey & Gaston 2006). Although conceptually well designed, this index requires decision steps (such as the choice of a distance metric combined with a clustering approach) and it is computationally demanding/unfeasible if there are millions of individuals in a dataset.

Other approaches do not require such decision steps and are less computationally expensive. Schleuter et al. (2010) reviewed different indices that describe the multidimensional trait space and their capacity to properly measure functional richness, evenness and divergence (Mason *et al.* 2005), demonstrating that some indices perform poorly. One example is the functional richness index FRic, which represents the volume of the minimal convex hull containing all species/individuals in a community (Villéger, Mason & Moullot 2008) and therefore includes gaps within the trait distribution (it is only sensitive to loss of species/individuals at the edges of the distribution). FRic therefore potentially disregards a large number of individuals (the ones not belonging to the vertices of the hull), and contradicts the broadest definition of TD presented above, in which TD should consider the information provided by all individuals within a community. Due to the flaws of FRic, Schleuter et al. (2010) proposed a new multidimensional functional richness index (FR_{lm}), which is based on the frequency distribution of trait values at the species level and is therefore not directly applicable to an individual-based context (Fontana, Jokela & Pomati 2014). Schleuter et al. (2010) have also shown that the evenness index FEve did not behave as expected from a measure of regularity in trait distribution.

The goal of this article is to test the indices that, according to *a priori* theoretical requirements imposed by the concepts and caveats of an individual-level perspective to TD (Fontana, Jokela & Pomati 2014), appeared to be the most promising for use with individual-level trait data (i.e. FRic, FEve, FDiv, FDis and the Rao coefficient). Additionally, we tested FD (Petchey & Gaston 2002; Petchey & Gaston 2006) (data not shown). Despite not

fulfilling all *a priori* requirements (see previous paragraph) and having restrictions in its applicability to all individual-level studies, it still performs well under certain circumstances and we added some comments about its behaviour in the Discussion. We also propose two novel TD indices for trait richness (TOP = Trait Onion Peeling) and trait evenness (TED = Trait Even Distribution), given the limitations of FRic and FEve in comprehensively describing changes in the internal structure of a multidimensional trait space, which emerge from this current investigation as well as from previous work. Note that all presented indices can also be calculated with species-level data, although we focus here on their applicability to individual-level data.

Materials and methods

Calculation of TD indices

The indices FRic, FEve, FDiv, FDis and the Rao coefficient were calculated with the software R (R-Development-Core-Team 2014) through the *FD* package (Laliberté & Legendre 2010). TOP uses the same mathematical principles of FRic (Villéger, Mason & Mouillot 2008), since it is based on the minimum convex hull concept (Cornwell, Schwikl & Ackerly 2006). However, instead of measuring the minimum convex hull volume (like FRic does), the richness index TOP represents the sum of all successive areas touching all the points in the trait distribution (Fig. 1). It is calculated as follows: after the first minimum convex hull containing the outermost points has been built and its area has been measured, these points are deleted from the trait distribution and a second convex hull is calculated with the new outermost points. This process continues, similar to peeling off layers of an onion, until the number of remaining points is insufficient for a convex hull (you need at least $n+1$ points to build a convex hull in a n -dimensional trait space). Since the number of individuals is typically much bigger than the number of traits considered, the influence of the remaining

points (besides the ones potentially accounting for the smallest area) can be considered negligible. The sum of all areas obtained in this way represents the TOP index, which is more sensitive to the loss of individuals at the edges of the distribution, but also considers changes in the middle of the cloud of data points. TOP is conceptually similar to the convex onion-peeling approach (Chazelle 1985; Abellanas *et al.* 1992), although it has been developed independently and for a different application in a multidimensional trait space.

The evenness index TED is a measure of how evenly distributed are individuals within the trait space (Fig. 2). It uses a reference distribution, obtained starting from equidistant (evenly distributed) points in n -dimensional space, where n is the number of traits considered. Although we chose a n -dimensional sphere with evenly distributed points as a model reference (*geozoo* R-package), it is possible to use any n -dimensional geometric shape provided that the same reference distribution is used for all communities for comparison. Since the number of points forming a n -dimensional sphere cannot be varied at will, the sphere with the lowest number of excess points relative to the test sample is automatically selected. Then, the outermost points in the distribution (the most distant from the centroid) are deleted, in order to obtain a cloud of evenly distributed points that is as similar as possible to a sphere, and has exactly the same number of data points as in the test sample. Distance matrices among all individual data points in the test sample and in the reference (even) distribution are calculated. Kullback-Leibler divergence (*KLdiv*) (Kullback & Leibler 1951; Kullback 1959) between these two probability distributions of distances (we used the default settings of density functions in R) is inversely proportional to the evenness of the test sample. Consequently, TED is calculated as

$$1 - \log_{10}(KLdiv + 1)$$

and its maximum value is therefore 1 (minimum *KLdiv* being 0). Although TED is generally positive, it does not have a minimum value, consistent with the concept of evenness in an

individual context, where regularity in a trait distribution can steadily decrease if one individual is distanced to infinity from the rest of the community. We admit that the choice of this formula is partially arbitrary, since it would be possible to obtain a maximum value of 1 with other formulas. It is important to note, however, that the validity of the general approach and concept is not dependent on specific methodological choices: the index would be computable even selecting e.g. non-default settings for some functions, a different approach for calculating the reference distributions or a different formula to compute trait evenness (for example $1/(1+KLdiv)$ or $\exp(-KLdiv)$ or $-KLdiv$ are possible alternatives). For more details on TOP and TED, we provide the R scripts as online supporting information.

Artificial test scenarios for TD indices

We first manipulated artificial data to test the responses of our candidate TD indices to changes in trait space. In every scenario, each coordinate axis corresponds to a measured trait and each point represents an individual organism (Fontana, Jokela & Pomati 2014). Two-dimensional (2-D) artificial scenarios are adapted from Schleuter et al. (2010) and three-dimensional (3-D) scenarios represent an extension of 2-D scenarios. Additionally, since we aim at finding reliable biodiversity indices for high-dimensional data, we tested eight-dimensional (8-D) scenarios with artificial data (maximum number of traits that remains computationally tractable given the large number of individuals in our datasets). Generally, trait data need to be standardised so that variation within each trait has the same importance (Petchey & Gaston 2006). In our case this was not necessary, because artificial trait values had the same unit.

In the different 2-D scenarios considered, trait values are integers between 1 and 8. We tested 2-D data in two different ways: in an addition scenario, starting with a community including 24 individuals, we added one individual with increasing distance from the centroid

of the distribution (for three different distances). In a removal scenario, starting with a community including 25 individuals, we removed nine individuals in different positions (Fig. 3). In the different 3-D scenarios considered, trait values are integers between 1 and 16. 3-D scenarios test the same changes as 2-D scenarios and are analogous to them, with some differences due to the additional dimension and the increased number of trait values: in the addition scenario, 27 individuals are added to an initial community of 1304 and in the removal scenario 343 individuals are removed from an initial community of 1331 (Fig. 4). Since the trait distribution in 2-D and 3-D scenarios is based, respectively, on a 2-D square and a 3-D cube, we used such figures (instead of 2-D circle and 3-D sphere) to build the even reference distribution for the calculation of TED. For testing trait richness and divergence, 8-D artificial data were represented by spheres with randomly distributed points (*geozoo* R-package). For testing trait evenness, the initial community was represented by a sphere with evenly distributed points (*geozoo* R-package), since this is the only approach that allows us to manipulate evenness. Although this initial community was obtained with the same method as the reference distribution for the calculation of the TED index, the two procedures have different purposes and should not be confused. The number of points in every sphere cannot be varied at will; therefore, all initial 8-D artificial communities contain 1713 individuals, which is the nearest possible number to the mean of real communities in this study (1689 individuals, see below).

Test scenarios for TD indices using real data

In order to ensure the practical applicability of our indices, we tested them with 8-D real phytoplankton monitoring data collected from Lake Zürich (Switzerland) during spring 2009 (Pomati *et al.* 2013). In that study, 15 water samples were analysed using the scanning flow-cytometer Cytobuoy (Woerden, the Netherlands; <http://www.cytobuoy.com>) as described

elsewhere (Pomati *et al.* 2013). We measured 46 descriptors of 3-D structure and fluorescence profile for each phytoplankton cell or colony. Since they are expressed in different units and some are cross-correlated, we performed a principal component analysis (PCA) and then retained eight orthogonal and standardised vectors, covering more than 85% of the total variance in the data, in order to obtain our 8-D traits. The 15 samples contained between 760 and 3275 individuals (mean=1689).

Manipulation of 8-D real and artificial data (scenarios S1-S9)

Scenarios S1 to S4 tested the effect of individual removal (1, 5, 10 and 20% of the total) from the edges and within the distribution of data on indices targeting trait richness: S1) removal of the outermost individuals (the most distant from the centroid of the community); S2) removal of the outermost individuals, not considering the ones belonging to the external convex hull; S3) removal of the individuals nearest to the centroid of the community and S4) random removal of individuals, not considering the ones belonging to the external hull. Scenario S5 tested the effects of random removal of 1, 5, 10 and 20% of the total number of individuals on indices targeting trait evenness. Scenarios S6 to S9 tested the effect of changing trait values of single individuals or a group of similar individuals (1, 5, 10 and 20% of the total) on indices targeting trait divergence, a property potentially related to selection and adaptation (Fontana, Jokela & Pomati 2014). S6-S8 moved different points outwards in trait space to double their distance from the centroid: S6) the outermost individuals (the most distant from the centroid of the community); S7) the innermost individuals (those closest to the centroid) and S8) a random selection of individuals. S9 moved similar individuals belonging to a single cluster (obtained by k-means clustering) by the distance between cluster centroid and overall centroid. In S9, the number of clusters was adapted to obtain at least one cluster containing enough individuals, since we did not move a whole cluster but 1, 5, 10 and

20% of the total number of individuals in the community; within each cluster, we moved the individuals most distant from the overall centroid. Among clusters with enough individuals (i.e. those containing 20% or more of the total number of individuals), the cluster with the smallest number of individuals was selected. Note that in scenarios with manipulation of randomly selected individuals (S4, S5, S8), as the percentages of individuals removed or moved increased, the individuals included in the lower percentage were removed together with additional (random) ones, in order to reach the next percentage. Fig. A1 in the Appendix shows a simplified representation of the different scenarios applied.

Correlation among TD indices and their sensitivity to sample size

We generated artificial 8-D communities to test correlations between indices and the influence of the number of individuals on every index, using an approach similar to Villéger, Mason & Mouillot (2008). Trait values of each individual were randomly selected from a uniform distribution between the minimum and maximum values of the first eight principal components of the real data. We generated communities with 100, 200, 300, etc. to 1000 individuals (total of 10 community abundance levels), with 100 replicates for each abundance level. TD indices were then computed for each replicate community. We used simple linear regression to explore the relationship between each pair of indices and between indices (mean value of 100 communities for every abundance level) and the number of individuals.

Expectations for the behaviour of TD indices in test scenarios

TD indices should respond to imposed changes in the distribution of individuals in trait space as expected by the formal definition of their properties (richness, evenness and divergence). Table 1 summarises the expected changes in individual-level trait richness, evenness and divergence under all considered scenarios (2-D and 3-D artificial data, 8-D artificial and real

data). Specifically, we expected trait richness to steadily increase from T1a to T1c, since every scenario represents the addition of one individual unique trait combination. The more distant the added individual is from the rest of the community, the wider is the range of trait space occupied, hence the higher the trait richness. According to the same principle, trait richness is expected to increase from T2a to T2c. On one hand, trait richness must be lower in T2a than in T2b, given the lower total range of trait space occupied. On the other hand, trait richness is expected to be higher in T2c than in T2a and T2b, although the three scenarios have the same number of individuals, since in T2c every trait value is present, while in T2a and T2b one trait value is missing.

In 8-D scenarios (Appendix, Fig. A1), our general expectations were decreased trait richness (and trait evenness for artificial evenly distributed data) if individuals were removed and increased trait divergence if the distance of individuals from the centroid was increased. We expect that the higher the percentage of manipulated individuals, the larger the change in the index value. Additionally, trait richness and divergence were expected to be more influenced by individuals that are more distant from the centroid (decreasing influence from S1 to S3, and from S6 to S7; not shown in Table 1).

Results

Table 2 summarises the observed changes in TD indices under all considered scenarios (2-D and 3-D artificial data, 8-D artificial and real data). More detailed results, including numeric values for artificial and real monitoring data (every single sample), are reported in the Appendix. The TOP index generally responded as expected, with very few exceptions (Table 2). In 2-D scenario T1a TOP did not show the expected increase (Appendix, Table C1), while in nine other cases it was not sensitive to changes in 8-D real data (Appendix, Table C4). On the contrary, FRic displayed a systematic flaw (Table 2): it was not sensitive to removal of

individuals that were not vertices of the external convex hull (Appendix, Tables C1, C2, C3). Since FDis and the Rao coefficient (trait divergence measures) seem to embed a richness component (Mason *et al.* 2013), we tested their responses also to scenarios targeting trait richness changes. FDis and the Rao coefficient performed poorly as trait richness indices in all scenarios (Appendix, Tables C1, C2, C5, C6). Consequently, in Table 2 the results of FDis and the Rao coefficient are summarised only as trait divergence indices.

TED performed clearly better than FEve (Table 2). FEve frequently did not change when it was expected to increase or decrease (red code in Appendix, Tables D1, D2), whereas TED always changed in the expected direction. However, the relative decrease of single T2 artificial scenarios (2-D and 3-D) did not always reflect the expectations (symbols between brackets in Appendix, Table D1). On the other hand, 8-D artificial scenarios fully reflected the expected changes in TED (Appendix, Table D2). FDis and the Rao coefficient showed very similar responses and the best performance among trait divergence indices (Table 2). Their changes generally reflected the expectations in 2-D, 3-D and 8-D scenarios, with only one exception (Appendix, Tables E1, E2, E4, E5): both FDis and the Rao coefficient decreased in 3-D artificial scenario T2b, when they were expected to increase. FDiv rarely performed as expected (Table 2; Appendix, Tables E1, E2, E3): its low accuracy was observed in all simulated scenarios (artificial 2-D, 3-D and 8-D, as well as real 8-D).

As expected, the TOP index, the FDis index and the Rao coefficient in 8-D scenarios were more influenced by changes in the individuals that were more distant from the centroid. The negative influence of individual removal on the TOP index decreased steadily from S1 (outermost individuals that represented vertices of the convex hull) to S2 (outermost individuals excluding the vertices) and from S2 to S3 (the nearest individuals to the centroid) (Appendix, Tables C2, C4). Analogously, FDis and the Rao coefficient were more positively

influenced when the outermost individuals were moved outwards in trait space (S6) than when individuals near to the centroid were moved (S7) (Appendix, Tables E2, E4, E5).

Discussion

Our results indicate that TOP is the best index for individual-level trait richness among the ones we tested because it shows the expected responses to changes in community trait structure, with rare exceptions that can be easily interpreted. In 2-D scenario T1a (Appendix, Table C1) TOP fails to increase because of the low number of dimensions and individuals (25 total): the addition of a single individual does not increase the number of layers (and corresponding calculated areas) in respect to initial scenario T1. The 3-D scenario with 27 individuals added (Appendix, Table C1), however, showed the expected response of TOP and is more likely to approximate real-world data (1331 individuals total). The nine single cases in which TOP does not respond to changes in 8-D scenarios with real data (Appendix, Table C4) are probably due to approximations of the results: depending on data structure, sometimes changes in the sum of the areas are not big enough to be reflected in the numeric result. On the contrary, FRic systematically failed to respond to changes in the middle of the trait distribution; this intrinsic flaw is clear from the index metric (convex hull volume) and confirmed by Schleuter et al. (2010), who showed that FRic is only sensitive to modifications at the edge of the trait distribution.

It is important to note that the use of the richness index FD (Petchey & Gaston 2002; Petchey & Gaston 2006) could be feasible when the computational efficiency is not a major issue. We tested FD in our scenarios of altered trait richness (data not shown) and, partially contradicting Schleuter et al. (2010), our results indicate that in 2-D and 3-D artificial scenarios, FD always changes in the expected direction (increase/decrease), however sometimes the magnitude of the change was not as expected. In 8-D artificial scenarios, FD

was more influenced by the removal of individuals nearest to the centroid of the community (scenario S3) than removal of outer individuals (scenario S2), whereas with 8-D real data, FD always responded as expected. In light of these results, we argue that FD is a reliable index of richness and, being sensitive to losses of individuals in the middle of the trait distribution, outperforms FRic. However, TOP still offers a more straightforward and computationally tractable estimation of trait richness, and as it requires only one decision step (selection of target traits), it is also a more objective measure of TD than FD.

Our results indicate that TED outperforms the other index of trait evenness (FEve). Unlike FEve, TED never remains constant when it is expected to increase or decrease (Table 2), although its relative decrease in some scenarios does not reflect the expectations (Appendix, Table D1). However, this potential drawback appears to be negligible for real-world multivariate data considering that it happens only in 2-D and 3-D scenarios, whereas observed responses in 8-D (more likely to approximate the dimensionality of ecological data) perfectly matched expectations (Appendix, Table D2). The low accuracy of FEve was already observed by Schleuter *et al.* (2010), who also suggested that FDiv is not a reliable trait divergence index. This was confirmed by all scenarios in our study.

Contrary to previous reports (Schleuter *et al.* 2010), our results on individual-level data suggest that FDis and the Rao coefficient are the best indices of trait divergence among those that we studied, although they decrease instead of increasing in 3-D artificial scenario T2b (Appendix, Table E1). Scenario T2b presents a large percentage of individuals grouped in a restricted volume of the trait space, because of the additional trait and the increased number of trait values (Fig. 4). That causes a shift of the centroid towards the majority of individuals and consequently a decrease in divergence. We think that the expectation previously put forward of an increase in trait divergence in a scenario like T2b (Schleuter *et al.* 2010) should be corrected to a decrease in a 3-D trait space, and both FDis and the Rao coefficient

represent accurate measures of functional divergence in all scenarios (2-D, 3-D and 8-D). Since FDis and the Rao coefficient are highly correlated (Appendix, Fig. B1) and therefore behave analogously, we suggest that FDis is preferable because its definition is more directly related to the concept of divergence, embedding distances from the centroid in the calculation (whereas the Rao coefficient considers pairwise distances between individuals).

In our study, all TD indices were demonstrably independent from each other, apart from FDis and the Rao coefficient (Appendix, Fig. B1; $R^2 = 0.98$): the correlations were very weak (R^2 ranging between 0.02 and 0.01) considering the large sample size ($n = 1000$). TOP was significantly and positively influenced by the number of individuals, whereas the other indices were independent of sample size (Appendix, Fig. B2). This is not surprising, and not necessarily undesirable, since Villéger et al. (Villéger, Mason & Mouillot 2008) found similar results for FRic. In our perspective, the correlation between TOP and the number of individuals is not problematic if the sampling effort is kept constant because a higher number of individuals increases the TD actually present and may have implications for community processes and resilience. Ideally, our proposed complementary approach would require the simultaneous evaluation of community changes in TOP, TED and FDis (the last two being independent of the number of individuals). If necessary, TOP can be bootstrapped to compare trait richness across sample sizes or different techniques can be used, e.g. functional rarefaction curves or nonparametric estimators (Ricotta *et al.* 2012; Cardoso *et al.* 2014).

In conclusion, corroborating and extending the results of Schleuter et al. (2010) to 3-D and 8-D scenarios, we recommend that FRic, FEve and FDiv should not be used for studies measuring individual-level TD. Instead, according to our results, we suggest that a set of complementary indices, encompassing all three TD components, be applied to individual-level trait data: the TOP index for trait richness, the TED index for trait evenness, and the FDis index for trait divergence. Such an approach, which considers the main components of

individual-level TD (Mason *et al.* 2005), is general and potentially applicable to all groups of organisms for which it is possible to measure traits at the level of individuals. Even if these indices directly use the objective information gathered by measurements, the only remaining decision step is extremely important: the selection of traits to be studied. Traits have already been recognised as the fundamental unit to explain ecosystem functioning even at a global scale (Reichstein *et al.* 2014) and individual-resolved models can explain ecosystem processes (Lasky *et al.* 2014). However, the selection and number of traits to be measured are dependent on the specific research questions. If traits are effectively related to the process of interest, even a small number of dimensions may reveal evident patterns in trait diversity indices. Since many ecological interactions (such as competition, predation, parasitism and facilitation) occur at the individual level, the ability to describe changes in the trait structure of a community may afford insight into trait dynamics and their consequences for larger scale ecosystem processes (Hillebrand & Matthiessen 2009; Reiss *et al.* 2009; Cardinale *et al.* 2012; Mason *et al.* 2013). For this reason, we are convinced that the set of trait diversity indices presented in this study will be useful for any researcher with individual-level data to take advantage of every piece of this information.

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Data Accessibility

Appendix and R scripts: uploaded as online supporting information.

Sample locations and trait data deposited in the Dryad Digital Repository:

<http://doi.org/10.5061/dryad.b28p8>, (Fontana, Petchey & Pomati, 2015)

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Table 1: Expected changes in traits richness, evenness and divergence under all considered scenarios. Since 8-D scenarios specifically target trait richness (S1-S4), trait evenness (S5) and trait divergence (S6-S9), expected changes are indicated only for the respective trait diversity component.

Table 2: Observed changes in TD indices under all considered scenarios. Although all TD indices have been calculated for all scenarios, for reasons of clarity and comprehensibility 8-D results are indicated only where expectations are available (Table 1). Scenarios are grouped when they show the same results (S2-S4, S6-S9). Where the 15 sampling dates of real data scenarios do not behave identically (TOP, FDis and the Rao coefficient in S2-S4, FDiv in S6-S9; Appendix, Tables C4, C5, C6, E3), the panel reports the number of occurring black/(black)/red dates (black = all 4 symbols for 1, 5, 10 and 20% of individuals are black; black between brackets = 0 red and at least 1 symbol between brackets; red = at least 1 red symbol). Total number of dates for S2-S4 is 45 (= 3 scenarios x 15 dates) and for S6-S9 is 60 (= 4 x 15).

Fig. 1: Simplified exemplification (2-D) of the calculation of the TOP index. Each red point represents an individual organism and its position is defined by different traits (axes). The perimeters of the five convex polygons (indicated with different colors) would represent areas of convex hulls in a multidimensional space. The TOP index of trait richness represents the sum of all areas.

Fig. 2: Representation of the steps required to calculate the TED index of trait evenness. The proposed example shows a community of 27 individuals distributed in a 3-D trait space. Each red point represents an individual organism and its position is defined by different traits (axes).

Fig. 3: All 2-D scenarios considered, adapted from Schleuter et al. (2010). Each red point represents an individual organism and its position is defined by different traits (axes). First row, we start with the community T1 (24 individuals) and added one individual with increasing distance from the centroid of the distribution (T1a, T1b, T1c). Second row, we start with the community T2 (25 individuals) and removed nine individuals in different positions (T2a and T2b: complete elimination of one trait value at the edge and within the distribution, respectively; T2c: removal in the middle of the distribution, maintaining all trait values).

Fig. 4: All 3-D scenarios considered. Each red point represents an individual organism and its position is defined by different traits (axes). Analogously to 2-D scenarios, 27 individuals are added (T1a, T1b, T1c) to an initial community of 1304 (T1) and 343 individuals are removed (T2a, T2b, T2c) from an initial community of 1331 (T2). Blue cubes are empty and indicate regions where individuals have been removed, exactly from the middle of the distribution. Violet shaded areas highlight added individuals.

		Trait Richness	Trait Evenness	Trait Divergence
2-D and 3-D artificial data	Scenario			
	T1a	+	+	-
	T1b	++	-	+
	T1c	+++	--	++
	T2a	---	-	-
	T2b	--	---	+
	T2c	-	--	++
	S1-S4 (1% individuals)	-		
	S1-S4 (5% individuals)	--		
8-D artificial and real data	S1-S4 (10% individuals)	---		
	S1-S4 (20% individuals)	----		
	S5 (1% individuals)		-	
	S5 (5% individuals)		--	
	S5 (10% individuals)		---	
	S5 (20% individuals)		----	
	S6-S9 (1% individuals)			+
	S6-S9 (5% individuals)			++
	S6-S9 (10% individuals)			+++
	S6-S9 (20% individuals)			++++

Legend

+/++/+++

Expected increase in the index compared to the initial reference community
(the number of symbols indicates the relative magnitude of change)

-/--/---

Expected decrease in the index compared to the initial reference community
(the number of symbols indicates the relative magnitude of change)

	Scenario	Trait Richness		Trait Evenness		Trait Divergence		
		FRic	TOP	FEven	TED	FDiv	FDis	Rao
2-D artificial data	T1a	+	+	+	+	++	+	+
	T1b	+	+	+	+	+	+	+
	T1c	++	++	+	++	+++	++	++
	T2a	+	+++	+	+	+	+	+
	T2b	+	++	+	(-)	+	+	+
	T2c	+	+	+	(-)	++	++	++
3-D artificial data	T1a	+	+	+	+	++	+	+
	T1b	+	++	+	+	+	+	+
	T1c	++	+++	+	++	+++	++	++
	T2a	+	+++	+	(-)	++	+	+
	T2b	+	++	+	(-)	+	+	+
	T2c	+	+	+	(-)	+++	+	+
8-D artificial data	S1 (1% individuals)	+	+					
	S1 (5% individuals)	++	++					
	S1 (10% individuals)	+++	+++					
	S1 (20% individuals)	++++	++++					
	S2-S4 (1% individuals)	+	+					
	S2-S4 (5% individuals)	+	++					
	S2-S4 (10% individuals)	+	+++					
	S2-S4 (20% individuals)	n/a	n/a					
	S5 (1% individuals)			+	+			
	S5 (5% individuals)			+	++			
	S5 (10% individuals)			+	+++			
	S5 (20% individuals)			+	++++			
	S6 (1% individuals)					+	+	+
	S6 (5% individuals)					++	++	++
	S6 (10% individuals)					+++	+++	+++
	S6 (20% individuals)					++++	++++	++++
	S7 (1% individuals)					+	+	+
	S7 (5% individuals)					++	++	++
	S7 (10% individuals)					+++	+++	+++
	S7 (20% individuals)					++++	++++	++++
	S8 (1% individuals)					+	+	+
	S8 (5% individuals)					++	++	++
	S8 (10% individuals)					+++	+++	+++
	S8 (20% individuals)					++++	++++	++++
	S9 (1% individuals)					+	+	+
	S9 (5% individuals)					++	++	++
	S9 (10% individuals)					+++	+++	+++
	S9 (20% individuals)					++++	++++	++++
8-D real data	S1 (1% individuals)	+	+					
	S1 (5% individuals)	++	++					
	S1 (10% individuals)	+++	+++					
	S1 (20% individuals)	++++	++++					
	S2-S4 (1% individuals)	+	As exp. 38x					
	S2-S4 (5% individuals)	+	(-) 3x					
	S2-S4 (10% individuals)	+	+					
	S2-S4 (20% individuals)	+	+					
	S5 (1% individuals)			n/a	n/a			
	S5 (5% individuals)			n/a	n/a			
	S5 (10% individuals)			n/a	n/a			
	S5 (20% individuals)			n/a	n/a			
	S6-S9 (1% individuals)					(+) 38x	+	+
	S6-S9 (5% individuals)					21x	++	++
	S6-S9 (10% individuals)						+++	+++
	S6-S9 (20% individuals)						++++	++++

Legend

+/++/+++
Expected increase in the index compared to the initial reference community
(the number of symbols indicates the relative magnitude of change)

-/-/-/-
Expected decrease in the index compared to the initial reference community
(the number of symbols indicates the relative magnitude of change)

n.a.
Not available data
(S2-S4 with 8-D artificial data: <20% of individuals are not vertices of the convex hull)

Black symbols
Change in the expected direction and relative magnitude

Black symbols between brackets
Expected direction but wrong relative magnitude

Red symbols
Wrong direction or unchanged index value "n"





